

XII. *Notes on the value of the genitalia of insects as guides in Phylogeny.* By W. WESCHÉ, F.R.M.S. Communicated by J. E. COLLIN, F.E.S.

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THE study of organs such as genitalia or mouth parts through a series of Orders has yielded much matter of interest, and the value of the mouth in classification has been fully recognised. A further investigation through the families of an Order is still more interesting, but it is a study beset with difficulties and pitfalls on every side. The material is so vast that the anatomist must pick his species, and suitable material is often not sufficiently abundant, especially in specialised forms. Conclusions derived from one form are obviously dangerous enough, but conclusions derived from the study of a number may be absolutely wrong when applied to a particular species. I have in my mind a typical case, where a very careful worker who had specialised on a particular family, denied the presence of two-jointed palpi in that family. As a matter of fact the vast majority of species are one-jointed, but at least three, of which one is a very common species in England, are two-jointed. This is the kind of danger which besets the worker in insect anatomy, and should be allowed for in estimating the value of his work. So if I now attempt some generalisations, I do so conscious of the difficulties of my endeavour.

Since the year 1900 I have made studies of the mouth parts and the genitalia of a number of species, and I have paid special attention to those contained in the Order Diptera.

A more general study of various families, selecting in each the most aberrant as well as the most widely distributed, or the most common species, shows that certain families are more conservative in type than others. But this conservatism may only apply to the mouth, while the genitalia are more variable, as is the case in the Syrphidæ; while in the huge group of the calyptrate Muscidæ, as long as the mouth remains unspecialised (a part ordinarily

most conservative in form), the male genitalia follow closely a common type.

Further, comparing family with family, one realises that cases of parallel development or degeneration occur. Many instances are found in the trophi; the mouth parts in *Conops*, certain Cyrtidæ, *Proscna* and *Glossina* are much alike in appearance, and the proboscis is formed in all cases from a modification of the under plate (mentum), and only differs in detail, yet this similarity is clearly no indication of affinity.

In the genitalia, the ovipositor may be especially modified and hardened into a boring apparatus as in the Phytomyzidæ, but a somewhat similar chitinising of the extremity in the viviparous *Phora ruficornis*, Mg., is no sign of relationship.

The degeneration of the wings is another similar character, and I think we must admit a tendency in the smaller forms in families, towards a simplification of the venation, and this must go into the same category. It is obvious that these parallel developments or degenerations must be recognised and ignored, when taking into consideration any Phylogenetic characters.

The lines of modification in the male genitalia all tend to two ends, an effective fertilisation of the female and an effective isolation of the species; so that these may come under the head of parallel developments, but as the second cause must result in very varied morphology, it can be excepted from the above generalisation. Indeed in these variations in the inner parts (the penis and its appendages) are to be found the more valuable Phylogenetic characters; the outer claspers (the forcipes superiores and inferiores of Dziedzicki) are sometimes of generic, but oftener only of specific value, as may be seen in *Anopheles* and *Tanyptus*.

In families which may be considered some of the oldest in the Nematocera, three types of penis are found: (1) a long styliform tube as in *Tipula*; (2) a prominent chitinous process with lateral processes, as in *Ptychoptera*; (3) and a low membranous process supported by lateral chitinous hooks or levers, as in the Australian genus *Gynoplistia* and in *Culex*.

Of these three forms the most striking is that of *Tipula*, and I think it can be clearly shown by methods of comparative anatomy, that modifications can be traced

through a number of families in the Nematocera and the Brachycera, and are in these cases useful Phylogenetic characters. It can be recognised in *Scatopse*, more particularly owing to the characteristic structure of the ejaculatory sac. *Pachyrrhina* has only specific differences from *Tipula*. In the Stratiomid Sarginae and Berinae great changes have taken place resulting in a shortening and thickening of the style, and a simplification of the ejaculatory apparatus; but the type remains the same, a chitinised process acting as a guide to a chitinised tube, which expands into an ejaculatory apparatus. Quite close to this are the forms of penis generally found in the Asilidae and Dolichopodidae, while in some species of *Empis* they are very near *Tipula* in the flagellum, and resemble the Stratiomyidae in the ejaculatory sac. The Pipunculid *Chalurus spurius*, Fln., also has a styliform penis, but differs in the ejaculatory sac which is membranous.

The extraordinary contradictions in characters, structures which are usually only found in the older families persisting side by side with late specialisations, show us that reliance cannot be placed on any single character as a test of Phylogeny. Whether that character be venation, mouth part, genitalia, shape or microscopic structure, unless supported by another character, it is apt to mislead.

This is demonstrable by comparison of the mouth parts of *Glossina* and *Stomoxys*; both are, as is well known, specialised for blood-sucking, and are somewhat alike in appearance and arrangement of the parts. The impression derived from a comparison of the male genitalia is very different; *Stomoxys*\* is close to the normal Muscid type, while in *Glossina* a remote and curious modification of that type is established, which appears to be a generic character, as I have found it common to the six species I have examined. The venation also shows that while *Stomoxys* approximates to the Cyrtoneurinae, *Glossina* is closer to the later Muscid type, as it is found in *Calliphora*, or as Mr. E. E. Austen points out to me, is nearly identical with the Cæstrid *Hypoderma*.

\* The late F. Tullock, in his paper "On the internal anatomy of *Stomoxys*," Proc. Roy. Soc., vol. 77 B, 1906, p. 525, describes the penis as of the "same type as *Glossina*." In the sense that both are Muscid in type, I am with him—but further I cannot follow, as the comparison suggests to me an extremely remote degree of relationship, or rather, a great divergence.

From this it can be seen that the presumption of close relationship suggested by the mouth is contradicted by the character of the male genitalia, and the venation only proves a family relationship. But when the extraordinary changes in the ovaries of the female of *G. palpalis*, Des., shown in Prof. E. A. Minchin's paper,\* *Stomoxys* remaining normal, are taken into consideration, together with many other points of structure external and internal, it is clear that *Glossina* and *Stomoxys* are far removed from each other.

A comparison of the Muscid species bearing specialised trophi, *Drymia*, *Stomoxys*, *Hæmatobia*, *Lyperosa*, *Proscna*, *Siphona*, *Glossina* and *Madyza* (the details of the argument are too long to quote here), has led me to the conclusion that these specialised mouths, like those of the genera already quoted, are cases of parallel development.

The genetal affinities between *Tipula*, *Scatopse*, the Stratiomyid genera, *Asilus*, *Dolichopus* and the Empidæ are supported by a similarity which is also a peculiarity, in the anatomy of the mouth. In families in which the mandibles are aborted, they are embedded in the labium.

(1) In the Tipulidæ it can be demonstrated that they are in the ventral side, as the lever on the dorsal side sends out processes to which the palpi are attached, which shows that they are the fused cardines and stipites of the maxillæ.

(2) In *Dolichopus* there is a marked thickening of the mentum on the median line and a structure showing the presence of atrophied or aborted organs. In the related *Aphrosylus raptor*, Hal., the mentum is simple and without this structure, but two chitinous blades can be dissected out of the muscles underneath it.

(3) In the Empidæ, Stratiomyidæ and *Scatopse* this character of a thickening of the chitin of the mentum on the median line is very marked.

(4) In the Asilidæ the mandibles are present, so the character fails, but the presence in the head of a structure, homologous with the pharyngeal pump in *Culex* and *Tipula*, connects it with the Empidæ and Dolichopodidæ, and so establishes the value of the genitalia character in all these instances.

The second type of penis, that found in *Ptychoptera*

\* Report on the anatomy of the Tsetse-fly (*Glossina palpalis*) Proc. Roy. Soc., vol. 76 B, 1905.

seems to foreshadow the Muscid type, in the symmetry and regularity of the lateral processes, while the forms found in *Culex* and *Gynoplistia* do not seem to be represented in later families.

The Tabanidæ and Leptidæ are closely allied on the venation, but far apart on the characters of the mouth parts, the details of structure being without suggestion of affinity, the mandibles having disappeared, and a much simpler armature being usually found in the latter family. The genitalia in *T. bromius*, L., ♂, are very complicated in the details of the ejaculatory apparatus, yet these complications are closely reproduced in *Leptis conspicua*, Mg., and with less difference than is often found between the species of the same genus.

Another point that suggests affinity is similarity of arrangement. In a number of families in Diptera, the hypopygium is turned in under the abdomen; but in only one, the Dolichopodidæ, and that only in certain genera, are the appendages that surround the penis displayed and disposed outside the cavity. An examination of the armature in the Phoridæ shows a prominent hypopygium, but the microscope shows that it consists of two portions, a segment supporting the anus and the representatives of the larger hooks (Dr. J. H. Wood's "anal protuberance"), and a second segment often with aculeations, containing the penis. This second segment, judging from numerous points of comparative anatomy, homologises with the appendages that surround the penis (theca), which are, as in *Dolichopus*, displayed outside the hypopygium.

This similarity of arrangement exists without the least trace of similarity of detail (unless it be in Conicera) or of structure suggesting affinity; but as there are striking points in the antennæ, the mouth and general structure that show an affinity between the Phoridæ and the Dolichopodidæ, the similarity of arrangement appears, especially as it is so singular, to be of Phylogenetic value.\* A remarkable development of the genitalia, both in the male and the female, in some of the Acalyptrate Muscidæ has been undervalued by systematists. It is true that in Osten-Sacken's list of 1878 and Verrall's British list of

\* In some rare cases asymmetrical forms of the inner parts are found, as in *Periplaneta*, and I have also found such a state in the "second" segment (the corresponding part) and its contents in some Phoridæ.

1901 the Ortalidæ, Trypetidæ and Lonchæidæ follow each other, but the horny telescopic ovipositor of the females and the remarkable development of the Muscid form of the male genitalia show that the differences between the three sections are only generic, and that they form one natural family. This opinion is strengthened by the character of the trophi, which is fairly constant through the group. In the labiums of the Ortalids *Scoptera vibrans*, L., and *Pteropæctria nigrina*, Mg., and the Trypetid *Acidia lychnidis*, F., are similar chitinous paired processes, which are peculiar and striking. This shows a very close relationship, and proves that a classification which places the two first insects in one family and the third in another, cannot be a natural one.

*The ovipositor.* Three types are met with in Diptera, (A) the telescopic or protrusile, (B) the non-telescopic, and (E) the styliform. The telescopic may be subdivided into (C) those with a framework of chitinous rods and (D) those without. The B type is undoubtedly the oldest and seems nearly universal in the Nematocera. A and B are both represented in the Muscidæ, but B is far oftener met with in the Acalyptrates. C seems confined to the Muscidæ, but examples of D may be met with in a few Syrphidæ, and in the Dolichopodæ, Phoridæ and Chloropodæ. In some Phoridæ the ovipositor has a lever to extend it, somewhat similar in shape to a process found in the non-telescopic ovipositor of the Simulidæ, and whose homologue appears to exist in a different form in the Chironomyidæ.

E. The styliform is found in the peculiar organ of the Pipunculidæ, but there are one or two aberrant forms such as *Phorocera serriventris*, Rnd., which I have come across in the Muscidæ, which might come under this head, but are really parallel developments. The types may be arranged in a Phylogenetic scheme placed in the order of hypothetical evolution, beginning with the oldest.

B. *Non-telescopic.*

E. *Non-telescopic* chitinised forms as in *Pipunculus*.

D. *Telescopic without rods* other than a single lever.

C (1). *Telescopic with many rods.\**

\* There are contained in the abdomen, parts of the female genitalia that strangely enough have characters. These are the receptacula seminis; they vary in number from one to four, have sculpturing on the cases, and may have characteristic shapes in certain genera, as in *Palloptera*, but their differences are mostly specific.

C<sup>(2)</sup>. Telescopic and with chitinised joints as in *Ortalida*.

*Conclusion.* I have already alluded to the difficulty of estimating a position in a systematic list brought about by the contradictions of characters, an archaic being contradicted by what we might call a late specialisation. But search will usually reveal an overwhelming balance on one side or the other, and it is usually the archaic character that stands. A comparison of two well-known flies will illustrate my point. The mouth parts and the male genitalia of *Calliphora erythrocephala*, Mg., and *Scatophaga stercoraria*, L., are absolutely homologous part for part, and quite close together in all respects. But *C. erythrocephala* has a telescopic ovipositor extended by rods, while in *S. stercoraria* it is non-telescopic. *Scatophaga* is undoubtedly the older type, and the wide space between the eyes of the male (Williston's *dichoptic*), the small calyptra, and the open first posterior cell of the wing confirm the older type of ovipositor.

To take a more difficult case, the Phorid *Trineura aterrima*, F., has an ejaculatory apparatus in the male genitalia, usually only found in the Muscidae. Against this, the species has dichoptic eyes, D type of ovipositor, no ptilinum, and mouth parts which have characters in the labium and mentum only found in the Brachycera and Nematocera, and a sense organ on the palpi practically exactly similar to that found in the Nematoceros *Dilophus*. The evidence is overwhelming that *Trineura* has no place, even in the older families of the Muscidae. We get collateral evidence when we find that other Phorids are without the ejaculatory sac and apodeme, and that the Pipunculid *Chalurus spurius*, Flh., together with a styliform penis, has a similar ejaculatory apparatus.

1. From these observations it may be assumed that those characters both of the male and the female genitalia, which are found in the Nematocera, when they can be recognised in other suborders, are the more reliable as guides in Phylogeny.

2. That a similarity of arrangement, when very exceptional and aberrant from the usual type, may also be relied on.

3. It can also be assumed that though genitalia cannot invariably be relied on to solve problems in Phylogeny, the evidence they afford is valuable and must be carefully

weighed, and they will always in the male afford specific characters.

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*Supplementary Note.* Since writing the above paper I have, with the aid of Dr. J. H. Wood, who has kindly supplied the material and notes on the external characters, made preparations and dissections of some Phoridæ which are included in Brues' genus of *Apiochæta*. The male genitalia throughout show a striking generic character in the presence of pads of chitinous cilia, supported by asymmetrical rods and rings, forming an organ of extremely complicated structure, whose minute size makes it difficult to study or understand, but I can in several species see the ejaculatory duct opening into the bases of the structures supporting the chitinous cilia. This arrangement is quite distinct from the apparatus found in such *Phora* as *incrassata*, Mg., or *curvinervis*, Beck., and appears to characterise the group and is good evidence in favour of the natural character of Brues' genus. It is interesting



that in the Chironomid *Tanyppus monilis*, L., I have also met with these pads of chitinous cilia in the genitalia, and also have been unable to find an external opening of the ejaculatory duct, but in this insect, unlike the Phoridae all the parts are symmetrical; the structure is so peculiar that it may be one more of the numerous links connecting the Phoridae with the Nematocera.